

CHAPTER 1

GENERAL INTRODUCTION

1.1 The pelagic ecosystem, a changing world

1.1.1 Defining the pelagic zone

The word *pelagic* is derived from the Ancient Greek (πέλαγος), meaning "open sea". The pelagic zone can be seen as a column of water that extends from the surface at the upper part of a water body almost to the sea floor. Deeper down the water column conditions change: pressure increases, temperature drops and light penetrates less. The water column can be divided into five horizontal layers depending on the depth. From top to down, these are: epipelagic (0-200 m), mesopelagic (200-1000 m), bathypelagic (1000-4000 m) and abyssopelagic (4000 m down to above the ocean floor). Around 99 % of the total ocean water volume is found below 100 m, and 75 % below 1000 m (Charette and Smith 2010, Costello *et al.* 2010). Worldwide, the pelagic zone occupies 1330 million km³ of water, based on a mean depth of 3.7 km and a maximum depth of 11 km (Charette and Smith 2010). Below the pelagic zone, one finds the benthic and demersal zones, with the benthic zone as the ecological region situated at the very bottom, including the sediment surface and some sub-surface layers, and the demersal zone situated just above the benthic zone.

The pelagic zone is the biggest habitat in the world (Costello *et al.* 2010). Not only is it big, it is also ecologically very important, since the vast majority of (pelagic and demersal) fish and many other species have a pelagic larval phase, including commercial fishes (Russell 1976). Small pelagic fish and many fish larvae tend to be largely dependent on zooplankton as their main food source. As such, zooplankton communities worldwide are critical to the functioning of marine food webs because of their sheer abundance, high diversity and vital ecosystem functions (Richardson 2008). Arguably, the most important role of zooplankton is as the major grazers in ocean food webs, providing the principal energy pathway from phytoplanktonic primary producers to consumers at higher trophic levels, including fish, seabirds and marine mammals (Mauchline 1998, Richardson 2008).

Pelagic organisms are thus mediating the functioning of the global ecosystem by influencing element cycling, biomass production and atmospheric composition (Duffy and Stachowicz 2006).

1.1.2 Human impact on the pelagic ecosystem

Of the many seas in the world, the North Sea ranks high in several aspects: there are many countries that influence the quality of North Sea waters, while the range of human activities (including fisheries, dredging, sand extraction, construction of windmills, *etc.*) it supports are vast. Laying on the European continental shelf and linked to the Atlantic Ocean, the North Sea is one of the most heavily fished areas in the world (Worm *et al.* 2009, FAO 2012). Large predatory fish are overfished and trawling has modified the benthic structure (Fig. 1).

Especially the southern North Sea - including its pelagic component - has been marked by more than a century of intense anthropogenic activities (Serchuk *et al.* 1996, Jackson *et al.* 2001, Vasas *et al.* 2007) (also see 1.1.3 and 1.2.2).

In the southern North Sea, depth rarely exceeds 80 m and the water column is often completely mixed (Horillo-Caraballo and Reeve 2008). The southern North Sea ecosystem, including the Belgian waters, is highly eutrophicated due to large nutrient inputs from anthropogenic sources through the discharges of major western European rivers (Lancelot *et al.* 1998, Rousseau *et al.* 2006). This leads to spring algal blooms and shifts in phytoplankton dominance from diatoms to the flagellates *Phaeocystis globosa* and *Noctiluca scintillans* (Lancelot 1995, Antajan 2004, Vasas *et al.* 2007). In a healthy marine ecosystem, herbivorous zooplankton normally controls such phytoplankton blooms, maintaining an equilibrium state (Rousseau *et al.* 2006). This is not the case in the southern North Sea, where algal blooms sustained by anthropogenic induced nitrates are suggested to be the result of losses in grazing activity by zooplankton. This reduced abundance of bottom-up controllers might have far-reaching and long-term effects throughout the food web (Lancelot *et al.* 2007), an effect exacerbated by chemical pollution and overfishing of planktivorous fish (Vasas *et al.* 2007) (Fig. 1).

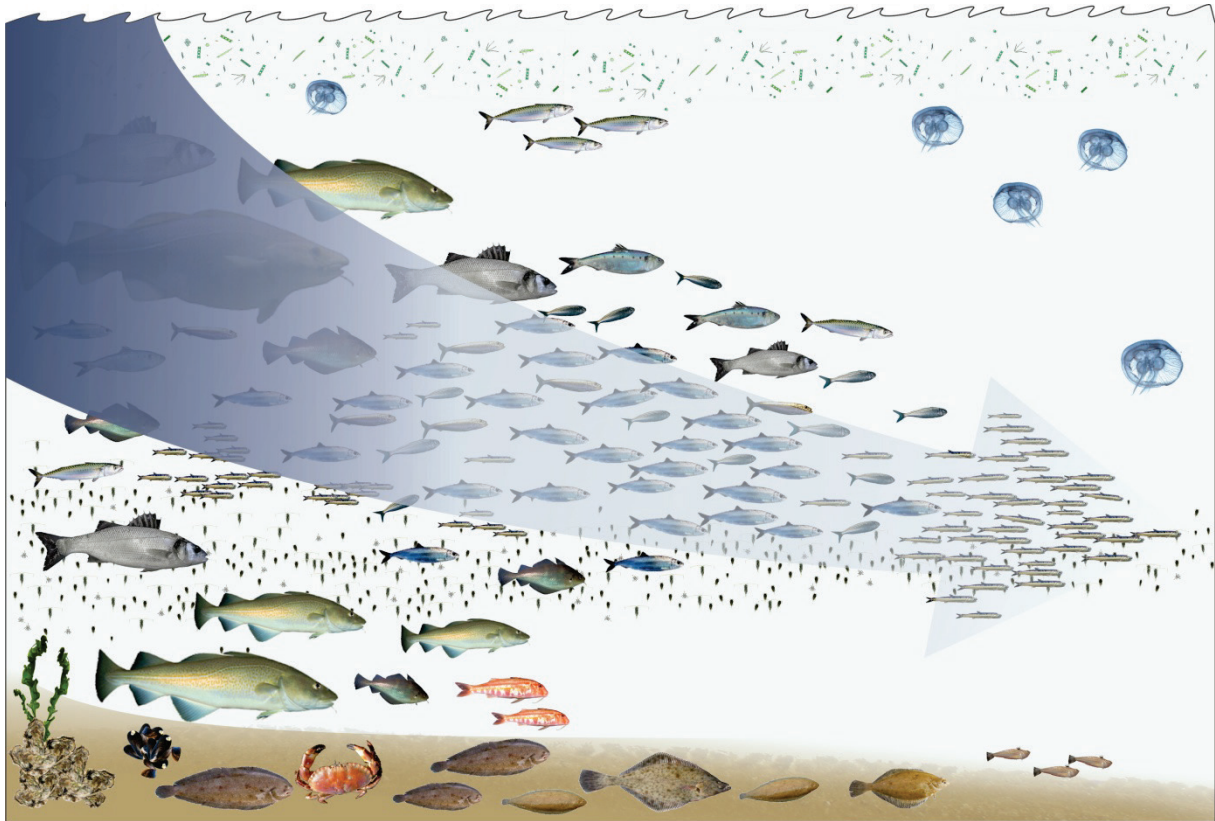


Figure 1: The future of the marine food web in de southern North Sea? Large predatory fish are overfished, trawling has modified benthic structure and the food web is evolving towards “a plankton soup dominated by opportunists and jellyfish”, Adapted from Pauly *et al.* 1998. © Hans Hillewaert

1.1.3 Climate change and the pelagic zone

Boyce *et al.* (2010) combined available ocean transparency measurements and in situ chlorophyll observations to estimate the phytoplankton biomass at local, regional and global scales since 1899. They observed a global decline rate of 1 % of the global median chlorophyll concentration per year. The authors postulate these long-term declining trends are to be related to increasing sea surface temperatures. Temperature tends to be a very important physical variable structuring all marine ecosystems (Richardson 2008). Planktonic organisms are exceptionally sensitive to temperature changes and it is this critical influence of temperature that makes pelagic ecosystems acutely vulnerable to global warming (Mauchline 1998, also see 1.2.2).

In the North Sea, monitoring projects by the Continuous Plankton Recorder (SAHFOS) from the 1940s to the present revealed large-scale and long-term changes in the abundance and phenology of plankton, also related to global warming (Lynam *et al.* 2004, Greve *et al.* 2005, Richardson 2008). Although such climate-related changes constitute a general pattern in the Northeast Atlantic, regional differences are noted. The North Sea temperature, for example,

has increased by 1.1 °C since 1962, but the southern North Sea is warming faster than the deeper northern basin (Wiltshire and Manly 2004, Hay *et al.* 2011). As such, temperate marine environments such as the southern North Sea are considered particularly vulnerable to global warming, because the recruitment success of higher trophic levels is highly dependent on the synchronization with the pulsed plankton production (Hjort 1914, Cushing 1990, Kirby *et al.* 2007). This can result in ecosystem-level changes (Edwards and Richardson 2004, Greve *et al.* 2005) when, for example, mismatches occur between taxa or processes regulated by temperature and others regulated by photoperiod (uninfluenced by changing climate) (Eilertsen and Wyatt 2000).

Moreover, species vary in their sensitivity, adaptive capability and response to environmental and ecological changes. The differential responses of species and species groups within the pelagic ecosystem will probably lead to a decrease in species abundance, biodiversity loss, introduction of species, mismatches between successive trophic levels, and influence the synchrony between primary, secondary, and tertiary production (Edwards and Richardson 2004, Richardson 2008). These changes influence recruitment, mortality, and the supply of resources to the benthic ecosystem and to higher predators such as fish, seabirds, and marine mammals (Lindley *et al.* 2002, Heath 2005, Frederiksen *et al.* 2006, Hay *et al.* 2011). Biological diversity plays a crucial role in the functioning of ecosystems and in the many services they provide (Vitousek *et al.* 1997, Loreau *et al.* 2001). Loss of marine biodiversity nationally, regionally and globally reduces the capacity of marine ecosystems to support the provision of goods and services, essential for human well-being (Cochrane *et al.* 2010).

1.2 Zooplankton, at the base of North Sea pelagic food webs

1.2.1 Classifying the zooplankton

Zooplankton are heterotrophic (rarely detritivorous) plankton. The word zooplankton is derived from the Greek “*Zoon*”, meaning animal, and “*planktos*”, meaning wanderer or drifter. The key feature is that plankton are passive drifters in oceans, seas and fresh water bodies, going where the currents take them. Although zooplankton are primarily transported by residing water currents, many have locomotion abilities to conduct vertical migration, to avoid predators or to increase prey encounters (Sieburth *et al.* 1978, Lalli and Parsons 1993).

Planktonic animals are often categorized in terms of **size**. The following divisions are used: femtoplankton ($< 0.2 \mu\text{m}$) $<$ picoplankton ($0.2\text{-}2 \mu\text{m}$) $<$ nanoplankton ($2\text{-}20 \mu\text{m}$) $<$ microplankton ($20\text{-}200 \mu\text{m}$) $<$ **mesoplankton** ($0.2\text{-}2 \text{ mm}$) $<$ macroplankton ($2\text{-}20 \text{ mm}$) $<$ megaplankton ($> 20 \text{ mm}$) (Omori and Ikeda 1992). We further distinguish zooplankton taxa according to their **lifestyle** in: **holoplanktonic** (spending their entire life as plankton in the water column, e.g. calanoid copepods), **meroplanktonic** (the early life stages, mainly from larger benthic animals, that spend a part of their life as plankters, e.g. decapod larvae), and **tychoplanktonic** taxa (which are occasionally carried into the water column, e.g. benthic species or species typical for the bottom part of the water column).

The zooplankton can also be divided in **coastal (neritic)** species, typical for shallow shelf areas, and **oceanic** species, typical for more offshore oceanic water masses. The North Sea and English Channel are part of the Northeast Atlantic Shelf Province (NASP), which extends from Spain to Denmark (Longhurst 1998). The NASP shows seasonal patterns classic for temperate regions: well-mixed conditions in winter, when nutrients are replenished but light is limited, followed by a strong spring plankton bloom, often becoming nutrient-limited when summer stratification sets in, and a smaller secondary bloom during autumn, as increased mixing breaks down the thermocline and nutrients are released again. This general Atlantic pattern is often broken up by locally strong tidal and shelf fronts, leading to permanently mixed water columns (Pingree and Griffiths 1978, Hay *et al.* 2011).

The North Sea is subject to inflow from Atlantic water currents, intruding into both the northern and southern part of the North Sea (Fig. 2) (Turrell *et al.* 1992, Howarth 2001). This Atlantic inflow, in terms of nutrient content, has a major impact on ecosystem productivity as it is estimated that 90 % of the annual nutrient input in the North Sea is derived from this source (NSTF 1993). Variability in the chemical properties, volume, biological content and source of the inflowing water regulate the North Sea ecosystem (Reid *et al.* 2003). In the Belgian part of the North Sea (BPNS), prevailing marine currents convey saline Atlantic water from the Continental Slope Current (and oceanic zooplankton) in a NE direction, where it meets the SW oriented Westerschelde outflow (Nihoul and Hecq 1984, Howarth 2001) (Fig. 2, 3).

The zooplankton communities in shelf areas such as the BPNS are usually a mixture of coastal (neritic) species, with a strong seasonal presence of meroplanktonic larval stages of benthic species (Beaugrand *et al.* 2002, Vezzulli and Reid 2003), combined with oceanic plankton species, that are occasionally imported with the inflow of oceanic water masses. Several of the common neritic species overwinter as resting stages, whereas other holoplankton species remain more or less active throughout the year (Richardson 2008).

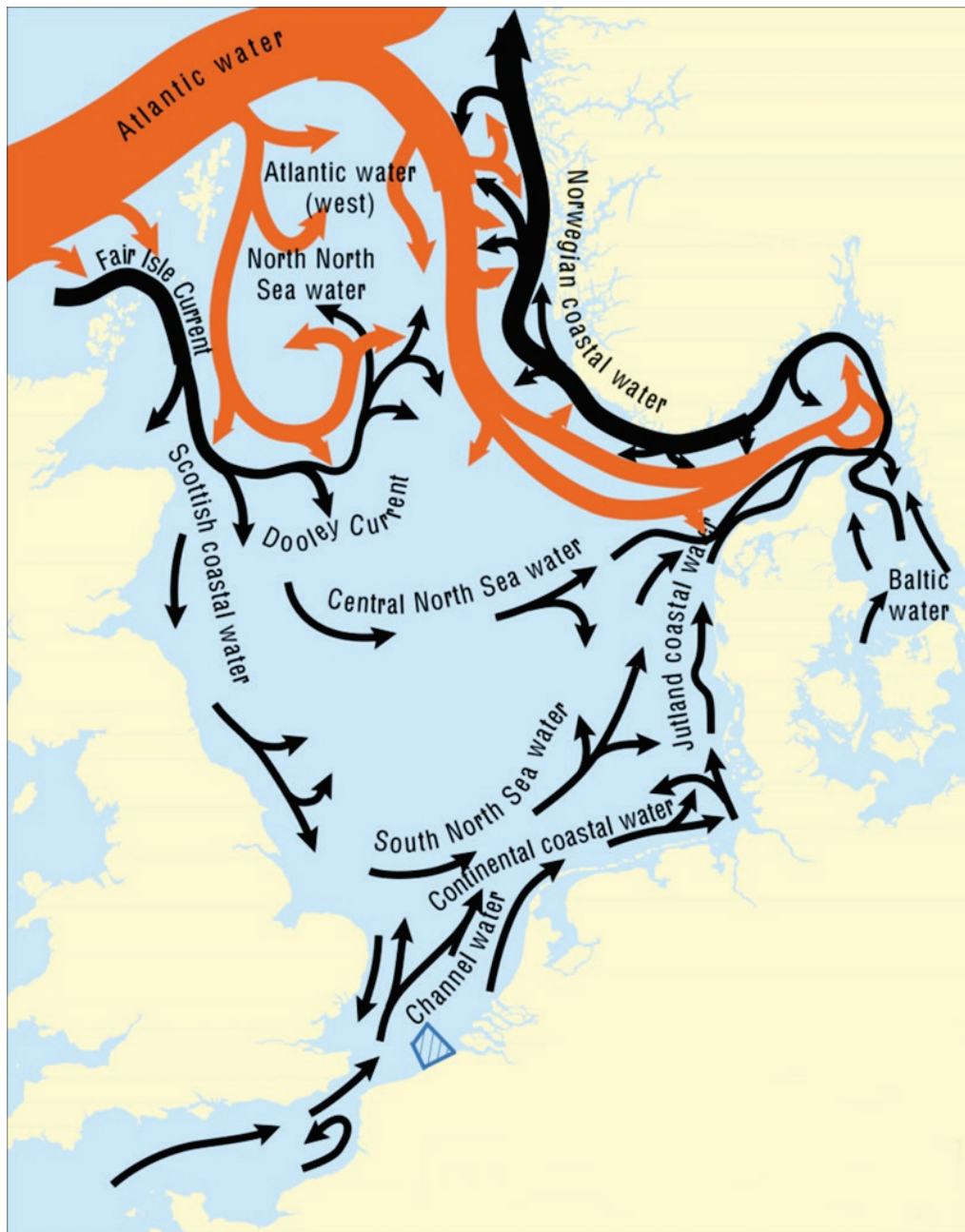


Figure 2: General circulation patterns in the North Sea. The width of the arrows indicates the magnitude of volume transport. Red arrows indicate Atlantic water seeping into the northern North Sea. A smaller continental slope current imports water through the English Channel into the southern North Sea. After Turrell *et al.* (1992). The BPNS is framed in blue.

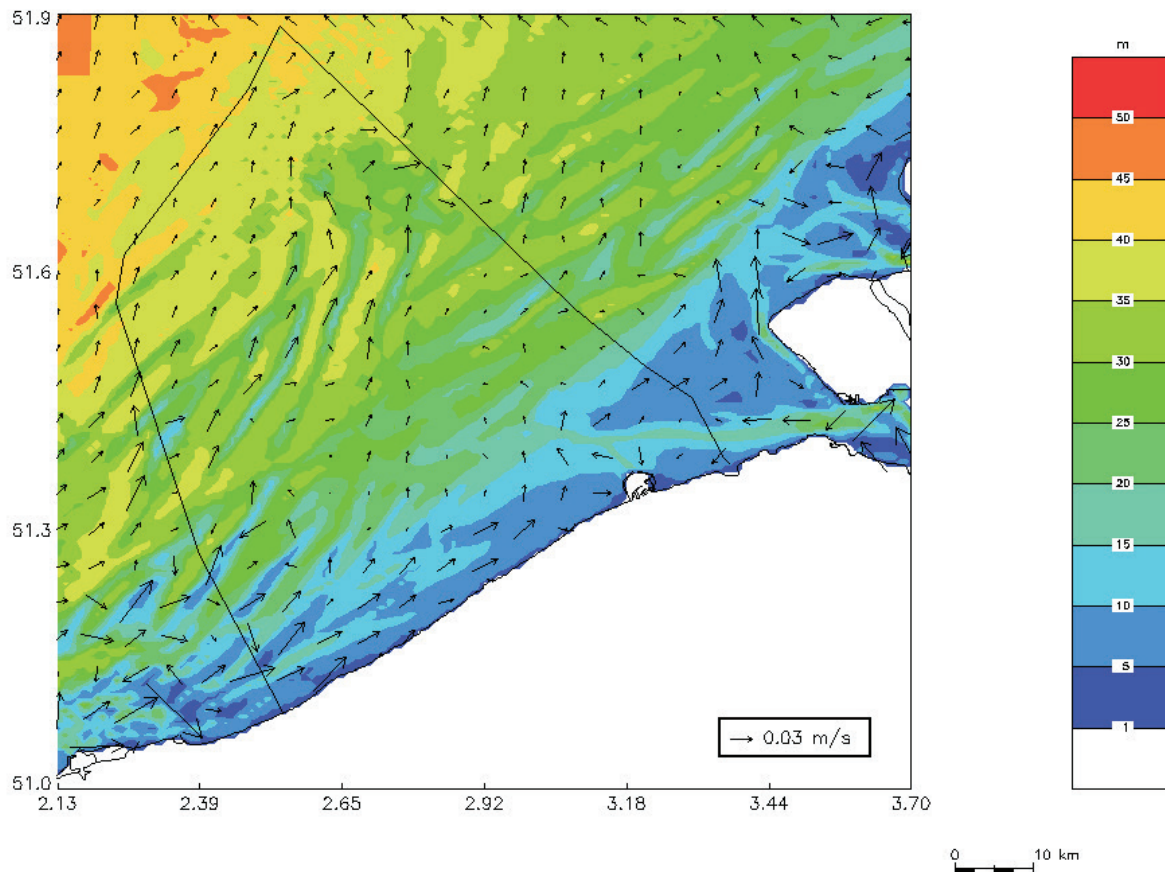


Figure 3: General circulation patterns in the BPNS, showing how the NE residual current interacts with the Westerschelde river outflow. Colors indicate depth (blue < green < red). Credit: MUMM.

The most prevalent zooplankton taxon consists of **copepods** (Crustacea), also the most abundant multicellular animals on Earth (Schminke 2007). In the southern North Sea, small calanoid copepods account for up to 84 % of the zooplankton abundance in spring and summer (Krause *et al.* 1995). Calanoid copepods generally fulfill a key role in marine food webs, transferring energy to higher trophic levels, but also to the benthic zone through sedimentation of faecal pellets (Nielsen *et al.* 1993). We refer to chapters 2 and 3 for an extended overview of North Sea plankton and copepods.

1.2.2 Zooplankton in relation to climate change

As carbon is fixed through faecal pellets, zooplanktonic organisms contribute in shaping the extent of climate change, but paradoxically, they are themselves very susceptible to a changing climate (Richardson 2008). The replacement of the cold water *Calanus finmarchicus* species assemblage in the southern North Sea by the warm water *Calanus helgolandicus* dominated copepod assemblage (with a different phenology, lower biomasses

and smaller species), is a textbook example of the severe consequences of the warming climate on marine ecosystems (Reid *et al.* 2003, Richardson 2008).

Zooplankton organisms can be described as beacons of climate change for a host of reasons (Richardson 2008). First, zooplankton are poikilothermic, implying their physiological processes (e.g. ingestion, respiration, reproductive development) are highly temperature dependant, with rates doubling or even tripling given a 10°C temperature rise (Mauchline 1998). Second, practically all zooplankters are short-lived (< 1 year), which allows for a tight coupling of climate and zooplankton population dynamics (Hays *et al.* 2005). Some suggest that plankton are more sensitive indicators of change than the environmental variables themselves, since the non-linear responses of planktonic communities might amplify subtle environmental signals (Taylor *et al.* 2002). Third, in contrast with fish and many benthic organisms, zooplankton organisms are seldom directly commercially exploited (exceptions are Antarctic krill and some jellyfish species), implying long-term studies on zooplankton linked to environmental change are less biased by any exploitation trend (Richardson 2008). Fourth, the majority of zooplankters are free floating, and remain so for the rest of their life. This means that the distribution of zooplankton can accurately reflect patterns in temperature and ocean currents.

Large seasonal and inter-annual variations are found in the phenology and densities of the dominant copepods. For example, at the Helgoland Roads zooplankton monitoring station (German Bight), a thirty year time-series revealed clear decadal variation in copepod numbers (Hay *et al.* 2011). Climate change can lead to concomitant biogeographical and phenological shifts in the distribution of planktonic species. Given the vital importance of zooplankton in the marine food web as link between primary producers and fish, birds and mammals, a thorough study on the spatial and temporal patterns in the zooplankton community in the BPNS, positioned in the transitional region between the Atlantic Ocean and the North Sea, is certainly justified.

1.3 Pelagic fish in the North Sea

1.3.1 Classifying the pelagic fish

In contrast with demersal fish, which live on or near the seafloor, pelagic fish permanently inhabit the water column. Like the zooplankton, marine pelagic fish can be divided into

coastal (inshore) and **oceanic (offshore)** species. Coastal fish inhabit the relatively shallow and sunlit shelf waters, whilst oceanic fish (which may occasionally swim inshore) inhabit the vast and deep waters past the continental shelf (Henderson 1989, Daan *et al.* 1990). Pelagic fish range in size from small coastal **forage fish** to large **top predators**. Forage fish or bait fish, such as herrings (Clupeidae) and sandeels (Ammodytidae) are preyed by many other species at a higher level in the food web. Large top predators, such as swordfish (Xiphiidae), tuna (Scombridae) and sharks (Selachii) are at the upper end of the food web. They are agile swimmers with streamlined bodies, capable of long distance migrations.

1.3.2 *Pelagic fish stocks in the North Sea: past and present*

Nowadays big pelagic top predatory fish are a rare sight in the North Sea, but this has not always been the case: MacKenzie and Myers (2007) showed that in the early 20th century majestic bluefin tuna *Thunnus thynnus* resided in European waters (northern North Sea, Norwegian Sea, Skaggeerrak, Kattegat and Oresund) for a few months each summer. When their presence became apparent, an industrialized fishery geared up in the 1920s and literally filled the floors of European market halls with tuna (Fig. 4). Long before the 1920s bluefin were being caught in southern Norwegian and Danish waters by vessels fishing in inshore grounds with long-lines and nets. These fish were large: many exceeded 400 kg and some were even larger (700 kg). In these days, the bluefin giants were mainly turned into pet food as there was no demand for the strange looking red tuna meat (Roberts 2007). *Anno* 2013, bluefin tuna is the most valuable fish species on earth with prices per fish often exceeding €100 000 on Tokyo fish markets. Imagine what a bluefin tuna stock still residing in the North Sea could mean for the public opinion, sustainable fishermen, environmentalists and policy makers: a true flagship species has disappeared from our waters.



Figure 4: Bluefin tuna fill a Danish auction hall, 1946 (Credit: Blegvad, H. Fiskeriet i Danmark).

Nowadays, the pelagic fish community in the North Sea and the English Channel mainly constitutes of mid-trophic smaller pelagics. Dominant species are herring *Clupea harengus*, sprat *Sprattus sprattus*, mackerel *Scomber scombrus*, horse mackerel *Trachurus trachurus* and lesser sandeel *Ammodytes marinus* and *A. tobianus*. Sandeels actually spend part of their time in the water column as pelagic fish and part in the seabed (Jensen *et al.* 2003). Species such as anchovy *Engraulis encrasicolus* and sardine *Sardina pilchardus* also occur in the North Sea and English Channel, but are seldom caught in the BPNS (Muus and Nielsen 1999). These abundant mid-trophic pelagic fish (often referred to as “**small pelagics**”) play an important role as staple food in marine ecosystems, channeling energy and nutrients between zooplankton and top predators (fish, seabirds, mammals). As such, pelagic fish are important and worth studying.

Small pelagic fish are also important targets for industrial fisheries (Frederiksen *et al.* 2006). The North Sea, laying on the European continental shelf and linked to the Atlantic Ocean, is one of the most heavily fished areas in the world (Worm *et al.* 2009, FAO 2012). As this study focuses on four small pelagic fish species, a summary on their current stock status in the North Sea is given. From 2000 to 2007, North Sea (autumn spawning) **herring** has produced eight poor year classes in a row and survival of larvae was poor (Payne *et al.* 2009). Gröger *et al.* (2010) linked herring productivity to climatic forcing of the North Atlantic, explaining the

reproductive failures using Atlantic climate oscillation indexes (NAO and AMO index). Currently, the herring stock is harvested sustainably and at full reproductive capacity, but the stock is still in a low productivity phase (ICES advice 2012). The safe biological limit is set at 0.8 million tonnes per year. The current status of the southern North Sea stock of **sprat** is unknown, but seems to be increasing and sustaining the recent catches (ICES advice 2012). Yet, the zooplankton that sustains sprat stocks in the northern North Sea seems to decrease (Beaugrand 2003, Reid *et al.* 2003, ICES 2006). The implications of this environmental change for North Sea sprat are yet unknown. The spawning stock biomass of the Northeast Atlantic **mackerel** is currently about 2.2 million tonnes. The mackerel stock is classified as having full reproductive capacity, but seems to be declining despite the record breaking strong year classes in 2005 and 2006 (ICES advice 2012). The exact status of the **horse mackerel** stock in the North Sea is unknown due to limited data, but it is advised that catches should not exceed $2.5 \cdot 10^4$ tonnes per year, as the stock appears to be declining since the early 2000s and has remained low since 2005 (ICES advice 2012).

It may seem strange given the current dominance of beam trawlers (> 90 %) in the Belgian fishing fleet, but herring actually used to be the first species commercially fished by Belgian fishermen in the 9th and 10th century (Rappé 2008). Lescrauwaet *et al.* (2010) elaborated on landings data and reviewed the evolution in pelagic fisheries by Belgian fishermen. During and after the second World War, very high landings of pelagic fish were reported with up to $5.8 \cdot 10^4$ tonnes (mainly herring) landed in Belgian fish auctions in 1943. At that time, pelagic fisheries focused on coastal waters, the southern North Sea and Fladen fishing grounds (northeastern UK). Not only herring but also sprat, mackerel and horse mackerel were targeted. The largest pelagic fish landings were achieved in the early 1950s ($2.1 \cdot 10^4$ tonnes in 1955), but after the last peak in the early 1980s ($0.9 \cdot 10^4$ tonnes in 1982) pelagic fisheries were considered the past (Lescrauwaet *et al.* 2010). Unlike the current large industrial pelagic trawling in the North Sea, the small scale pelagic fishery in the BPNS required detailed skills and knowledge, with several vessels working together by pair trawling to land a single catch (Rappé 2008). Anno 2013, Belgian fishermen no longer target pelagic fish, but several Dutch ship owners bought Belgian licenses and fish for non quoted species such as mackerel, horse mackerel and red mullet *Mullus surmuletus* in Belgian waters by means of flyshooting (an encircling seine net put on the seafloor attached to long cables, who scrape

the floor and stir fish into the net). As such the Dutch fishermen prove that fishing small pelagics in the BPNS is still profitable.

1.4 Pelagic fish in relation to climate change

The four pelagic fish species in this study are important commercial fish. Therefore, a better understanding of their ecology is crucial. Oceanographical spatial and temporal processes impose strong drivers on pelagic fish and their trophic interactions. Sea surface temperature, thermocline depth, presence of coastal fronts and currents (e.g. variable inflow of Atlantic water) have significant effects on the distribution and abundance of fish species (Iversen *et al.* 2002).

The climate change we are currently experiencing, invokes fluctuations in the oceanic conditions, which influences the status of North Sea pelagics, as following examples illustrate. As already shown above, North Sea (autumn spawning) herring produced eight poor year classes in a row between 2000 and 2007, and the survival of larvae was low (Payne *et al.* 2009). This low productivity of herring was linked to the climatic forcing of the North Atlantic by Gröger *et al.* (2010). Another example is given for Atlantic mackerel. In 2011, Icelandic and Faroese catches of Atlantic mackerel amounted up to 32 % of the total reported landings, whereas this species was rarely caught in Icelandic or Faroese waters prior to 2008 (ICES advice 2012). It is thought that climate forcing is currently pushing mackerel north, leading to higher catches. A third example comes from the Helgoland Roads zooplankton time series. Observations in 1990–1999 revealed that planktonic fish larvae are extremely sensitive to temperature changes, leading to shifts in their seasonal distribution. No less than 30 % of the studied species showed a significant correlation between their peak in abundance and the mean water temperature (Greve *et al.* 2005). A final example is given for Atlantic cod *Gadus morhua*, a very valuable commercial species in the North Sea. Atlantic cod spawn in spring, and their larvae grow best on a diet of large copepods. If these are absent from the water column, mortality is high and cod recruitment is poor. In the southern North Sea the calanoid copepod *Calanus finmarchicus* has been replaced by *C. helgolandicus* (see 1.2). Despite the fact that these *Calanus* congeners are morphologically almost indistinguishable, they have contrasting seasonal cycles: *C. finmarchicus* densities peak in spring, whereas *C. helgolandicus* peaks in autumn (Bonnet *et al.* 2005). Since the late 1980s,

the virtual absence of *C. finmarchicus* resulted in a lower copepod biomass during spring and summer in the North Sea, leading to a nadir in cod recruitment (Beaugrand *et al.* 2003).

1.5 The role of zooplankton in the pelagic food web

Pelagic (and demersal) fish species must keep in step with their zooplanktonic food sources, for this is what the fish and their larvae eat (Muus and Nielsen 1999). Determining trophic interactions between zooplankton and pelagic fish requires diet and feeding rate studies. Diet composition reflects feeding ecology, while shifts in diet may be linked to either climate control, anthropogenic impacts, seasonality or inter-annual variations. Major changes in diet of pelagic fish have been documented on seasonal and inter-annual time scales (Dalpadado *et al.* 2000, Gislason and Astthorsson 2000, Hanson and Chouinard 2002). Also daily variations in diet and feeding intensity have been examined (Köster and Schnack 1994, Albert 1995, Darbyson *et al.* 2003), and mismatches between predatory fish and prey due to climate change have been reported (Cushing 1990, Southward *et al.* 1995).

A short literature overview on the diet of the four studied fish species is given below (also see chapter 4). Studies comparing the feeding ecology of several fish species were carried out in the Baltic Sea (Arrhenius 1996, Möllmann *et al.* 2004, Bernreuther 2007), the Barents Sea (Huse and Toresen 1996), and the Norwegian Sea (Bromley *et al.* 1997, Prokopchuk and Sentyabov 2006).

The diet of Atlantic **herring** is widely accepted as being dominated by planktonic crustaceans (Hardy 1924, Arrhenius and Hansson 1992, Dalpadado *et al.* 2000, Darbyson *et al.* 2003, Möllmann *et al.* 2003, Segers *et al.* 2007). Most important copepods in the diet are *Calanus* spp., *Temora* spp. and *Pseudocalanus* spp. Other important constituents are fish eggs (Hardy 1924, Segers *et al.* 2007), amphipods, chaetognaths, and urochordates (Hardy 1924, Bainbridge and Forsyth 1972, Daan *et al.* 1985). Adult herring are considered to be visual feeders (Batty *et al.* 1990), hence they start foraging above a certain light threshold (Legget and Deblois 1994). Spatial differences in prey selectivity are noted (Savage 1937), and herring feeding schools are often associated with feeding mackerel Holst *et al.* (2004).

Sprat diet consists of copepods, crustacean larvae, cladocerans, *Oikopleura* spp., mysids and euphausiids (De Silva 1973). Sprat usually shows prey selectivity (Sandström 1980, Raid 1985,

Hansson *et al.* 1990). As sprat and herring both feed on pelagic crustaceans a possible competition for planktonic food sources may occur on the BPNS.

The diet of **mackerel** usually contains copepods, other pelagic crustaceans and small fish, such as herring, sprat and sandeel (Mehl and Westgård 1983). Mackerel feeding patterns may vary seasonally and spatially, and they are known to stop feeding almost completely during winter (Mehl and Westgård 1983).

Immature **horse mackerel** are found to feed on pelagic euphausiids and copepods (Macer 1977). Fish larvae and juveniles, such as 0-group herring, cod and whiting (5-7 cm long) become more important in the diet of bigger horse mackerel, as they start feeding more demersally (Eaton 1983, Dahl and Kirkegaard 1987).

1.6 Pelagic research in the southern North Sea

The southern North Sea maintains a wide range of ecosystem based anthropogenic activities, such as fisheries, aquaculture, energy production, aggregate extraction, transport and tourism. It is one of the most studied marine areas on earth (Hay *et al.* 2011).

For zooplankton, most data for the North Sea are provided by the Continuous Plankton Recorder (CPR) surveys (conducted since the 1940s). The aim of the CPR Survey is to monitor the near-surface plankton (both phyto- and zooplankton) of the North Atlantic and North Sea, using continuous plankton recorders attached to industrial ships. Uniquely, the methods of plankton sampling and analysis of these CPR surveys have remained unchanged since 1948, providing a spatio-temporally comprehensive > 60 year database of marine plankton dynamics (Warner and Hays 1994). This has led to > 230 papers published in international literature.

The CPR covers a vast area (Fig. 5), but just a limited part of it is studied on a yearly basis (Fig. 6) and only the surface water layers are sampled, instead of the entire water column. The device itself has a very narrow entrance aperture of 1.6 cm², which makes it less likely to catch big and faster plankters (Haddock 2008). More detailed info on the seasonal variation in certain areas is provided by time series from several zooplankton monitoring stations in the North Sea and English Channel (Fig. 7): Helgoland Roads (German Bight, since 1975), Plymouth L4 (western English Channel, since 1988), Dove (western central North Sea, since the mid-1970s), Stonehaven (northwestern North Sea, since 1997), Arundel (eastern central North Sea, since 1994), and the recent Loch Ewe station (northwest Scotland, since 2002)

(Hay *et al.* 2011). These time series, together with the CPR have proven of utmost importance when quantifying and studying climate change and its effect on the North Sea ecosystem. Only very recently (January 2013), the monitoring station at Gravelines (English Channel, sampled by IFREMER) was added to the -publicly available- COPEPODITE zooplankton monitoring metabase (Fig. 7). There are no data from this station in the earlier ICES zooplankton status reports but monthly sampling results will be provided in the future (Pers. Comm. Elvire Antajan, IFREMER).

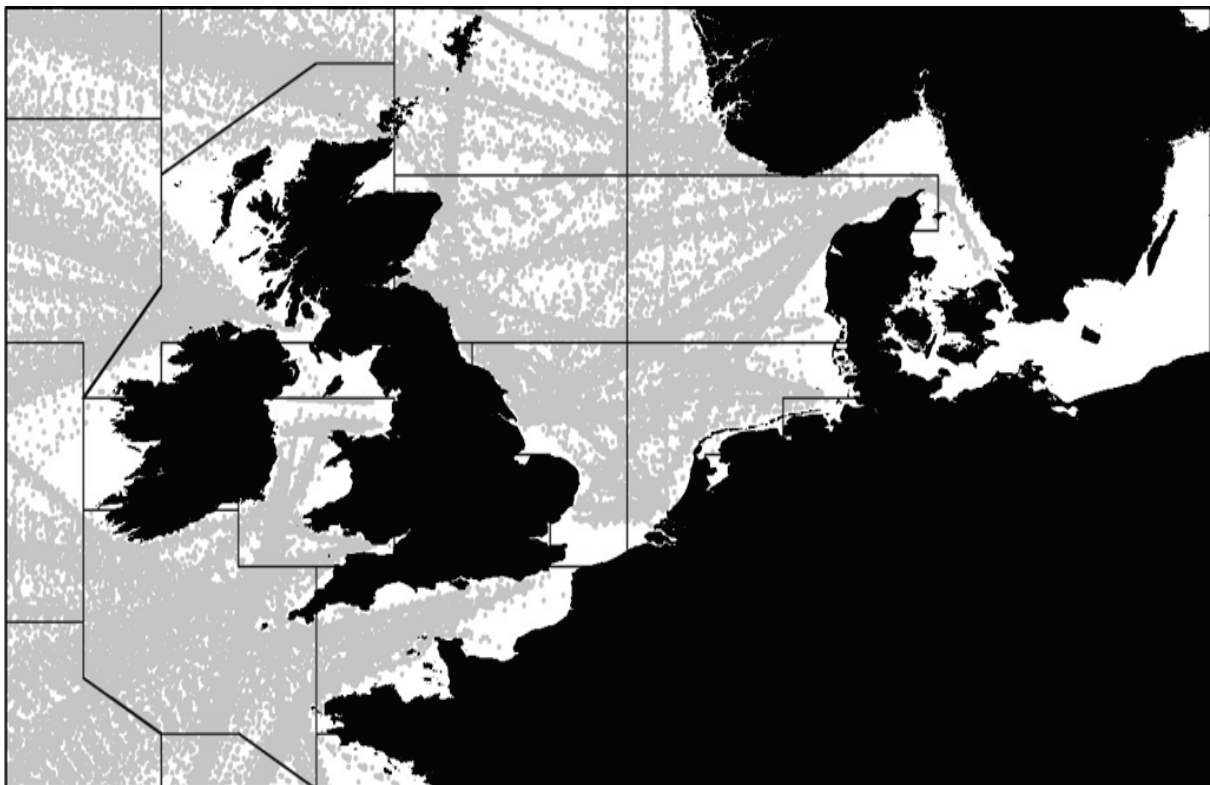


Figure 5: All available CPR trawl data in the eastern Atlantic. Notice that the eastern English Channel and southern North Sea remain poorly sampled (Credit: SAHFOS).

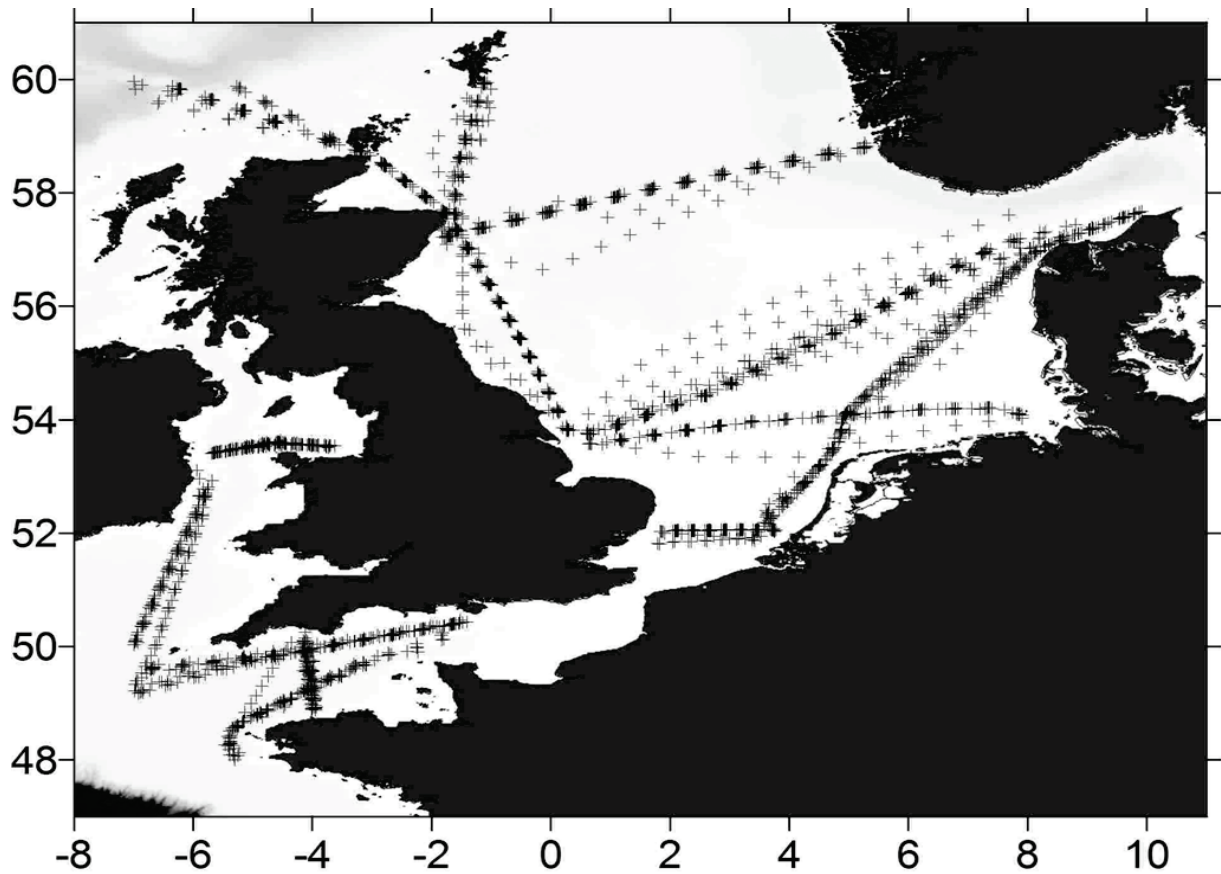


Figure 6: CPR trawls in 2009 and 2010 in the North Sea and English Channel (Credit: SAHFOS).

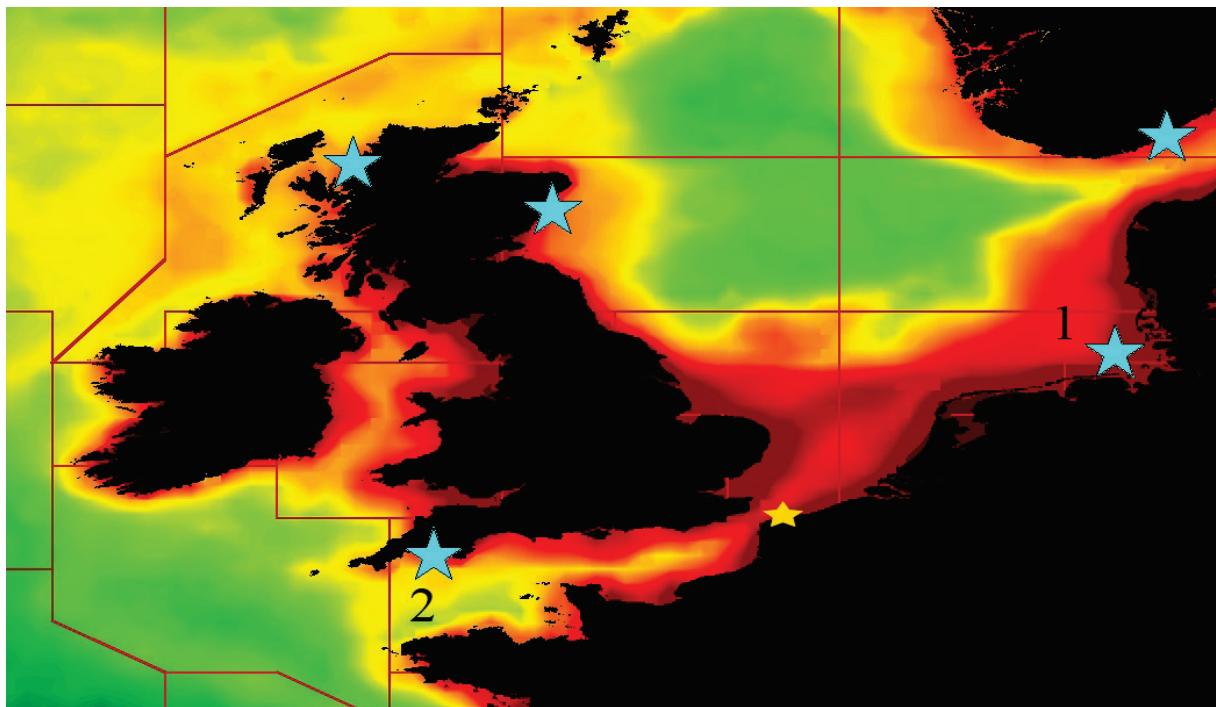


Figure 7: Location of North Sea and English Channel zooplankton monitoring stations (blue stars), plotted on a map of average chlorophyll concentration (green < yellow < orange < red). Monitoring stations closest to the BPNS are Helgoland Roads (1) and Plymouth L4 (2) (O'Brien *et al.* 2011). The yellow star indicates a sampling station (Gravelines) that joined the copepodite zooplankton database recently in January 2013.

In total, > 500 papers have been published on North Sea zooplankton. A detailed literature overview on zooplanktonic studies in and around the BPNS is provided in chapters 2 and 3. Still, there is a clear lack of CPR samples from the English Channel and southern North Sea (Fig. 5, 6) nor exists a monthly monitoring station in the vicinity of Belgian waters, which could allow for a detailed temporal analysis. From the many European studies on zooplankton it is difficult to pool or compare results, as a wide variety of gears and mesh sizes was used, or sampling was limited to only one month or a fixed depth.

Concerning pelagic fish, *ca.* 600 papers have been published on herring, sprat, mackerel and horse mackerel from the North Sea. Next to yearly estimates of their stock sizes (ICES advices 2012), many papers investigated the fish diets (see chapter 4).

Despite the vast amount of literature on North Sea zooplankton and pelagic fish, a study on pelagic fish and zooplankton, simultaneously sampled every month during consecutive years, spanning nearshore to offshore sampling locations, has not yet been performed in the southern North Sea. Taking into account the commercial value of North Sea pelagic fish, and the current biogeographical and phenological shifts in the distribution of the pelagic fish and their zooplanktonic prey, an update on pelagic fish feeding ecology in the Belgian part of the North Sea is certainly in place.

The scientific value of this doctoral thesis lies in the fact that we could not only look into the zooplanktonic community structure of the BPNS with great temporal and spatial detail, but also link the *in situ* plankton results (*i.e.* the prey availability) directly to the stomach contents (*i.e.* the diet and selectivity) of four pelagic fish species.

1.7 Objectives and outline of the thesis

The aim of this PhD thesis is to expand and update the knowledge on the mesozooplankton community structure in the southern North Sea, and to characterize the trophic role of zooplankton as prey for pelagic fish in the North Sea food web.

In an attempt to close the identified gaps in available data and information, this study focused on the following objectives:

1. Which zooplankton species are present and which species are new for the Belgian part of the North Sea? Which non-indigenous species are present and what densities

are reached by the different zooplankton species? How are the zooplankton communities spatially and temporally structured?

2. Which are the dominant pelagic fish species in the BPNS, and what is their diet? Are there spatial and temporal patterns in their diets?
3. Is there a correlation between the zooplankton present in the water column and the diet of four pelagic fish species in the BPNS, allowing us to draw conclusions on bottom-up control by plankton organisms or selective foraging behavior by small pelagic fish.

In Chapter 2, an extensive inventory and update of the zooplankton species list is given for the Belgian part of the North Sea (BPNS). Assessing species abundance and diversity is crucial to address several descriptors of the current European Marine Strategy Framework Directive. We focused on both the dominant and rare species, as well as on non-indigenous zooplanktonic species. We briefly discuss the distribution of the zooplankton community and focus on the presence/abundance of all taxa separately. This paper acts as a state-of-the-art and ready to use zooplankton checklist of the BPNS. The last part of this chapter describes the discovery of the non-indigenous ctenophore *Mnemiopsis leidyi* in Belgian waters.

In Chapter 3, the spatial and temporal distribution patterns in the zooplankton community of the southern North Sea are updated. Monthly data from 2009 and 2010 were used to investigate whether one or several zooplanktonic communities were to be distinguished. Results on the dominant holo-, mero-, and tychoplankton species, and the contribution of neritic vs. oceanic species are presented. We investigated whether calanoid copepods could play a key role in the food web, and which patterns in zooplankton distribution could be identified. The results on zooplankton were compared to the distribution patterns in other ecosystem components (demersal fish, epibenthos and macrobenthos) presented in other studies on the BPNS. This allowed us to formulate general conclusions on the presence of a species- and abundance-rich zone in the BPNS.

In Chapter 4, results on the diets of herring *Clupea harengus*, sprat *Sprattus sprattus*, mackerel *Scomber scombrus* and horse mackerel *Trachurus trachurus* in the BPNS are presented. The stomach content analyses were related to the zooplankton distribution and

to the prevailing abiotic conditions, a task that was accomplished over a near-mid-offshore gradient and two complete seasonal cycles. We focused on differences in composition, sex and life stages of the different zooplankton species in the water column, compared to those in the fish stomachs. Selectivity in pelagic fish feeding behavior and bottom-up regulation/restriction by zooplankton are discussed. We investigated whether planktonic prey densities (\approx food supply) were highest in the same seasons and stations, as when peaks in fish stomach fullness were calculated.

In Chapter 5, the main results of this PhD study are discussed in a broader context. We discuss not only what we discovered, but also what still is to be investigated, to further unravel the pelagic ecosystem and the relation between goods and services the pelagic provides. The implications of our results for policy and conservation purposes and for the pelagic research in the Belgian part of the North Sea are explored. The chapter ends with some major conclusions on the zooplankton community structure and the role of zooplankton in the pelagic ecosystem of the BPNS. Finally, several remaining challenges concerning the pelagic research in the southern North Sea are put forward.